CALORIFIC VALUES IN THE PHYLUM PLATYHELMINTHES: THE RELATIONSHIP BETWEEN POTENTIAL ENERGY, MODE OF LIFE AND THE EVOLUTION OF ENTOPARASITISM

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An analysis of the calorific values (kcal/g) of seventeen species of animals from six phyla has shown that they have a skewed distribution with a modal frequency at or near the lower range limit (Slobodkin and Richman, 1961). This was regarded as support for the hypothesis that natural selection generally favors production of the maximum number of progeny, rather than a high energy content per unit weight. The latter is favored only sporadically and under special circumstances such as preparation for a period of fasting or stress (Slobodkin, 1962).

To test this hypothesis further we have undertaken a survey of calorific values within the Platyhelminthes. This phylum shows a broad spectrum of life styles which range from the free-living predatory habits of most Turbellaria, through various degrees of facultative or obligate ecto- or entocommensalism (other Turbellaria), to the obligate ecto- or entoparasitism of a few Turbellaria and all Monogenea, Digenea and Cestoda (Jennings, 1971; 1973). The symbiotic species show high fecundity relative to the free-living forms (Hyman, 1951), apparently as an adaptation to their mode of life, and by the above hypothesis could be expected to have correspondingly lower calorific values.

The entosymbiotic species also differ from the free-living ones in that they contain large amounts of carbohydrate, usually in the form of glycogen. This accounts for up to 17.73% of the dry weight in entocommensal turbellarians, 14.77% in digeneans and 26.99% in cestodes, but only 9.96% in free-living flatworms (data from various sources, summarized by Jennings, 1973). The latter, though, generally store lipid and levels of up to 19.83% of the dry weight have been recorded (Jennings, 1957; Mettrick and Boddington, 1972). This dichotomy in the form in which potential energy is stored has long been regarded as stemming from differences in the oxygen tensions of the environments of free-living and entosymbiotic species. Habitats within other organisms, and especially alimentary tracts, often have low oxygen tensions (Campbell, 1931; von Brand, 1946; Rogers, 1949; Crompton, Shrimpton and Silver, 1965) and in such situations carbohydrates may well be the most appropriate metabolic substrates. There is certainly much evidence, ably reviewed by Read (1968), that many parasitic flatworms have metabolic processes suited to life under semi-anaerobic conditions. However, as Crompton, *et al.*, 1965 emphasize, the partial pressure of oxygen in regions favored by entosymbiotes still usually exceeds the value of 5 mm Hg given by Hill

(1936) as the threshold necessary for satisfactory functioning of cytochrome oxidase. Further, some entosymbiotes live in fully aerobic situations and yet store glycogen (Halton, 1967; Mettrick and Jennings, 1969), so that this phenomenon cannot be linked directly with oxygen tension. Recognizing this, Jennings and Mettrick (1968) have suggested that glycogen storage, instead, is linked in some way with high fecundity. Carbohydrates, having lower calorific values than lipids (Cummins and Wuychek, 1971), may reduce whole body values for the ento-symbiotes and this notion therefore conforms to the hypothesis cited by Slobodkin and Richman (1961) that fecundity generally implies a low calorific value.

Consequently, in addition to testing the general applicability of this hypothesis, by examining calorific values in the phylum Platyhelminthes, we have also examined the validity of its particular implications for entosymbiotic animals. This has been done by selecting species for examination which are representative of the various life styles in this phylum so that any correlation between potential energy and mode of life would be revealed.

Material and Methods

The species investigated are listed systematically together with some details of their habitats and modes of life. The few species for which calorific values have already been published are also listed, with the authority, since the data for these will be incorporated with those from the present study.

Turbellaria

Rhabdocoela

Syndesmis franciscana (Lehmann). Entocommensal in the gut and coelom of *Strongylocentrotus purpuratus* Clark (Echinoidea), from Bodega Bay, California.

Allococoela

Plagiostomum sulphureum von Graff. Free-living, marine littoral, Filey Brigg, Yorkshire, England.

Tricladida

Bdelloura candida (Girard). Ectocommensal on the gills and limbs of *Limulus polyphemus* L. (Xiphosura), Cape Cod, Massachusetts.

Dendrocoelum lacteum (O. F. Müller). Free-living, freshwater littoral, Loch Lomond, Scotland.

Dugesia lugubris (O. Schmidt). As *D. lacteum*.

Planaria torva (O. F. Müller). As *D. lacteum*.

Polycelis nigra (O. F. Müller). Free-living, freshwater littoral, Malham Tarn, Yorkshire, England.

Procerodes ulvae (Diesing). Free-living, marine littoral, Isle of Cumbrae, Scotland.

Bipalium kewense Moseley. Free-living, terrestrial. Data from Slobodkin and Richman, 1961.

Dugesia tigrina (Girard). Free-living, freshwater littoral. From Slobodkin and Richman, 1961.

Phagocata gracilis (Haldeman). As *D. tigrina*. From Minshall, G. W., unpublished data, cited in Cummins and Wuychek, 1971.

Phagocata morgani (Stevens and Boring). As *D. tigrina*. From Teal, 1957.

Phagocata woodworthi Hyman. As *D. tigrina*. From Teal, 1957.

Monogenea

Polyopisthocotylea

Diclidophora merlangi (Kroyer). Ectoparasitic on the gills of the whiting *Gadus merlangus* (L.) (Teleostei), Whitby, Yorkshire, England.

Entodbella soleae Johnston. Ectoparasitic on the skin of the sole *Solea solea* (L.) (Teleostei), Plymouth, England.

Polystoma integerrimum Rudolphi. Entoparasitic in the urinary bladder of *Rana temporaria* L. (Amphibia), Adel, Yorkshire, England.

Digenea

Prosostomata

Fasciola hepatica L. Entoparasitic in the biliary system of domestic sheep *Ovis aries* L. (Mammalia), slaughtered in Glasgow, Scotland.

Haplometra cylindracea Looss. Entoparasitic in the lungs of *Rana temporaria* L. (Amphibia), Adel, Yorkshire, England.

Cestoda

Cyclophyllidea

Hymenolepis diminuta Rudolphi. Entoparasitic in the intestine of laboratory rats, *Rattus norvegicus* Berkenhout, Wistar strain (Mammalia), Department of Zoology, University of Toronto.

Pseudophyllidea

Triaenophorus nodulosus Pallas. Entoparasitic in the intestine of the pike *Esox lucius* L. (Teleostei), R. Ouse, Yorkshire, England.

Tetraphyllidea

Echeneibothrium variable Van Beneden. Entoparasitic in the spiral valve of the skate *Raia clavata* L. (Elasmobranchii), Whitby, Yorkshire, England.

The four freshwater species of triclads (*D. lacteum, D. lugubris, P. torva* and *P. nigra*) were kept in the laboratory for two weeks prior to examination and fed daily on the oligochaete *Tubifex,* apart from one subgroup of *P. nigra* which were starved for this period. All other species were processed immediately after collection from the field, or removal from their hosts.

Calorimetry

Living healthy specimens were rinsed briefly in distilled water and then either freeze dried to constant weight (*Syndesmis franciscana* and *Hymenolepis diminuta*)

TABLE I

Calorific values (kcal/g ash-free dry wt), Joule equivalents and ash contents of free living and symbiotic Platyhelminthes

Species and mode of life	kcal/g ash-free dry wt ± 95% conf. interval	kJ/g ash-free dry wt	Ash % dry wt ± 95% conf. interval**	Number of measurements
Free living				
D. lacteum	6.316 ± 0.317	26.439	5.82 ± 0.39	10
D. lugubris	6.295 ± 0.222	26.351	3.50 ± 0.27	10
P. nigra	6.420 ± 0.338	26.874	6.10 ± 0.71	10
P. sulphureum	6.798†	28.456	7.71 —	1
P. torva	6.382 ± 0.451	26.715	3.79 ± 0.42	10
P. ulvae	6.000 ± 0.258	25.116	6.95 ± 0.72	3
B. kewense	5.684 ± 0.124	23.793	*	*
D. tigrina	6.286 ± 0.338	26.313	*	*
P. gracilis	6.377 ± 0.137	26.694	*	*
P. morgani	5.600†	23.442	*	*
P. woodworthi	5.600†			
Mean	6.216 ± 0.258	26.019	5.65 ± 0.41	
Ectocommensal				
B. candida	5.897†	24.685	10.09†	1
Entocommensal				
S. franciscana	5.080 ± 0.216	21.265	11.72 ± 2.35	3
Ectoparasitic				
D. merlangi	5.372†	22.487	8.98†	1
E. soleae	5.668†	23.726	6.10†	1
Mean	5.520	23.107	7.51	
Entoparasitic (except Cestoda)				
F. hepatica	5.205 ± 0.201	21.788	5.07 ± 0.37	10
H. cylindracea	5.124†	21.449	6.53†	1
P. integerrimum	5.372†	22.487	5.98†	1
Mean	5.234 ± 0.292	21.908	5.85 ± 0.15	
Cestoda				
E. variable	5.164 ± 0.316	21.616	3.86 ± 0.39	5
H. diminuta	5.817 ± 0.203	24.350	4.30 ± 0.41	10
T. nodulosus	5.972†	24.999	2.17†	1
Mean	5.651 ± 0.561	23.655	3.44 ± 0.67	
Grand mean for all species	5.841 ± 0.230	24.452	6.17 ± 0.08	

† = insufficient material for replicates.

* = data from other authors, % ash and number of measurements not specified.

** = data were transformed to arcsines before calculation of mean and confidence intervals, and have been retransformed for presentation (Rohlf and Sokal, 1969).

or air dried at 60° C for twenty four hours. The dried specimens were ground into powder and calorific values determined for the entire animal. In *H. diminuta* individuals were also divided into three portions, consisting of immature, mature

and gravid proglottids and each portion was then processed separately to detect any differences in energy reserves related to the different reproductive states.

Calorific values were determined in a Phillipson micro-bomb calorimeter using standard calorimetric techniques (Phillipson, 1964). Each sample used was of at least 10 mg dry weight and usually was in excess of 15 mg. Routine corrections were applied for fuse wire "glow" and acid production (Paine, 1971). The ash contents were usually less than 10% of the dry weight (only four samples had > 10% ash) and consequently no correction was applied for endothermy (Paine, 1966). Due to the small size of most of the specimens and the difficulties of obtaining suitable numbers there was not, in most cases, enough material for independent determination of ash content in a muffle furnace. This information was routinely obtained, therefore, from the residues remaining in the bomb after firing. Data were discarded if fuse wire contamination was suspected.

Replicate samples were used whenever the amount of material available permitted. When possible, up to ten subsamples were examined, means were computed together with fiducial limits and the latter were corrected for small sample sizes (*i.e.,* t. $\frac{s}{\sqrt{n}}$, where t was obtained at the 95% probability level for $n - 1$ degrees of freedom). Means for species with common modes of life were then averaged. Data were compiled in this fashion because it was considered that the resultant means and variances were of greater importance than those based on individual measurements.

Calorific values for free-living triclads obtained by previous investigators were used either directly (*e.g.,* those for *B. kewense* and *D. tigrina* given by Slobodkin and Richman, 1961), or after adjustment to make them comparable with those obtained here. The values given by Teal (1957) for two species of *Phagocata* were obtained by dichromate digestion and expressed in terms of wet weight. To obtain an ash-free dry weight estimate it has been assumed, from experience in drying samples, that dry weight equals 25% of wet weight and that ash equals 5% of dry weight (the average ash value for the four freshwater triclads studied here being 5.038% as calculated from the data in Table I).

Results

The potential energy contents of the 21 species of flatworms investigated are listed in Table I, together with their ash contents expressed as a percentage of the dry weight. Energy values are given in terms of kcal/g ash-free dry weight and S. I. (Joule) equivalents are also shown. Fiducial limits on the calorific values ranged between 2.14–7.06% of the means, which is generally considered to be acceptable for biological samples.

Before considering these results in detail it should be pointed out that, apart from random manipulative errors, two further factors may have influenced the data. First, no correction has been made for nitrogen production during combustion. This may have resulted in an underestimate of the calorific values, but since there appears to be little interspecific variation in nitrogen contents within the Platyhelminthes (Mettrick and Boddington, 1972) comparative treatment of the data is still legitimate (Kersting, 1972). Secondly, bomb combustion, rather than muffle furnace estimates of ash, can introduce systematic errors into calorific
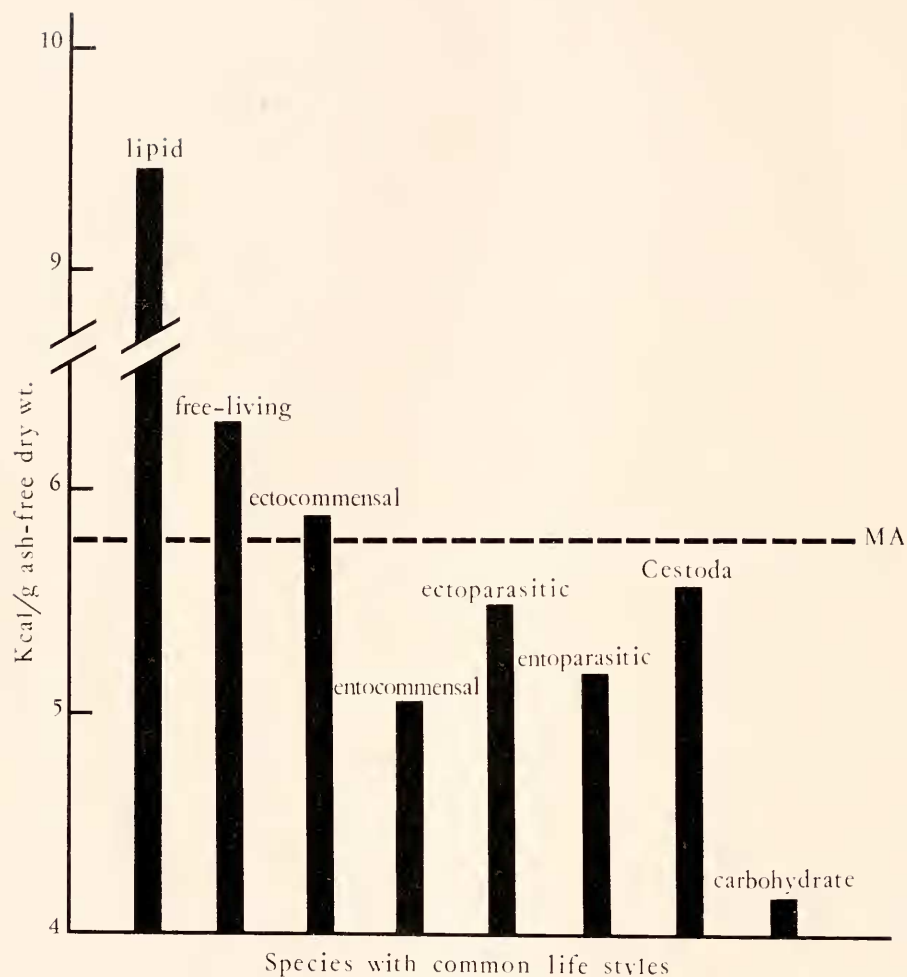
FIGURE 1. Mean calorific values (kcal/g ash-free dry weight) of flatworms with common life styles. The values for lipid, carbohydrate and MA (the mean value for whole animals from other phyla) are from Cummins and Wuychek (1971).

values. However, this depends on the ash content of the materials involved and becomes more extreme as percentage ash increases. At ash levels below 10% (most of the species considered here) the effect becomes trivial and contributes less than ± 1% variation (Reiners and Reiners, 1972).

The grand mean of 5.841 ± 0.230 kcal/g ash-free dry weight for all the species studied falls close to the mean value of 5.821 kcal/g ash-free dry weight previously reported for whole animals from a wide range of other phyla (data summarized by Cummins and Wuychek, 1971). Values ranged from a minimum of 5.080 kcal/g ash-free dry weight for the entocommensal *S. franciscana* to a maximum of 6.798 kcal/g ash-free dry weight for the free-living *P. sulphureum*.

The mean calorific values for species sharing common life styles are summarized in Figure 1. This shows that the free-living flatworms have a value higher than the mean for whole animals from other phyla (MA) whereas the entocommensal and entoparasitic species, other than cestodes, have much lower values. The ectocommensal, ectoparasites and cestodes, however, have values very close to this mean.

The differences in calorific values and ash contents between the three regions of the cestode *H. diminuta* are shown in Table II, together with values for the whole worm. The calorific values of immature and mature proglottids are similar to each other, but significantly smaller than that of the gravid proglottids (d = 2.53, $P \simeq 0.02$). The value for the whole worm is only slightly less than that of the gravid component and is obviously elevated by this. The immature and mature proglottids are more comparable to the whole flatworms of other classes, in terms of growth and reproductive activity, than are the gravid proglottids and the mean calorific value for these two regions (5.554 kcal/g ash-free dry weight) is somewhat closer to those for the entocommensal and entoparasitic species than is the value for whole cestodes.

Figure 1 also shows average calorific values for pure lipids and carbohydrates. The range between these two extremes represents that which is theoretically possible in organic material but the actual range recorded here within the Platyhelminthes is considerably less. This is also the case in all other organisms so far studied (Cummins and Wuychek, 1971).

Starvation for two weeks caused a significant fall in the calorific value of the free-living triclad *P. nigra*. The value dropped from 6.420 kcal/g ash-free dry weight to 5.050 kcal/g ash-free dry weight, and the ash content fell from 6.10% dry weight to 5.98%. The average size decreased by approximately 30%.

Discussion

Calorific values in the Platyhelminthes follow the general pattern observed in other phyla in that they are skewed towards the lower possible limit (*i.e.* the value for carbohydrate, Figure 1), with a mean of 5.841 kcal/g ash-free dry weight and a range of 5.080–6.798 kcal/g ash-free dry weight. The distribution within this range, however, is not haphazard but shows a definite relationship to the mode of life. Entosymbiotic species, with the exception of the Cestoda, have values which cluster towards the lower limit of the range and are generally less than the mean level for animals from other phyla (MA of Figure 1 and referred to hereafter as "mean animal"), whereas values for the free-living flatworms cluster toward a higher level and have a mean in excess of that for the "mean animal." The ectosymbiotes and cestodes are intermediate between these two extremes.

Fluctuations in ash-free calorific values around the "mean animal" level have been identified almost exclusively with fluctuations in tissue lipid concentration (Ostapenya and Sergeev, 1963). This is because proteins and carbohydrates have similar energy equivalents (*circa* 5.7 and 4.1 kcal/g ash-free dry weight, respectively), while lipids have far greater equivalents (*ca.* 9.5 kcal/g ash-free dry weight). Thus our results confirm that the evolutionary trend within the Platyhelminthes, assuming that the free-living forms are primitive, has been toward a reduction in the amount of lipid stored per unit weight with a concomitant reduction in calorific values.

The cestodes are somewhat atypical, when compared with the other ento-symbiotes, in that they have relatively high and variable calorific values (Table I). The latter probably result from variability in lipid contents; high lipid levels have been reported in *Hymenolepis diminuta* by Webb and Mettrick (1973) but much lower levels are recorded for several other cestodes (Smyth, 1966). In *H. diminuta* gravid proglottids contain a higher proportion of lipid than do immature and mature ones (Fairbairn, Wertheim, Harpur and Schiller, 1961; Mettrick and Cannon, 1970) and this is reflected in their high calorific value (Table II). If the cestode strobila is viewed as a series of progressively maturing reproductive units, though, rather than as a single individual, it becomes legitimate to compare only the immature and mature proglottids with the whole individuals from other flatworm groups. The gravid proglottids contain the products of reproduction and are more comparable, therefore, to the cocoons of free-living flatworms. The immature and mature proglottids have calorific values closer to those of other ento-symbiotes than does the whole cestode (Table II) and so conform more closely to the basic evolutionary trend in the phylum.

TABLE II

Calorific values (kcal/g ash-free dry wt.), Joule equivalents and ash contents in Hymenolepis diminuta

	kcal/g ash-free dry wt $\pm 95\%$ conf. interval	kJ/g ash-free dry wt	Ash $\%$ dry wt $\pm 95\%$ conf. interval	Number of mea-surements
Whole worm	5.817 ± 0.203	24.35	4.30 ± 0.41	10
Immature proglottids	5.559†	23.27	3.30†	1
Mature proglottids	5.550 ± 0.241	23.23	3.54 ± 0.39	8
Gravid proglottids	5.997 ± 0.185	25.10	3.35 ± 0.28	10

† = insufficient material for replicates.

The link between calorific value, fecundity and mode of life would seem, therefore, to be amply demonstrated in the Platyhelminthes. The precise nature of this link is at first difficult to define, but the situation becomes clearer when it is recognized that "survival of the fittest" must be interpreted in terms of the survival rate of offspring rather than entirely in terms of survival of the adult. Thus the "fittest" individual is one which produces the greatest number of viable offspring, and selection will operate in favor of using any energy available in excess of growth and maintenance requirements for progeny production rather than for accumulation of endogenous food stores. In Slobodkin's words "there is a selective advantage in increasing fecundity but not adiposity" (Slobodkin, 1962, page 71). From this viewpoint it is the free-living flatworms which are atypical in the Platyhelminthes and the onus is put on explaining their high calorific values, resulting from lipid stores, rather than on explaining the low energy equivalents, resulting from glycogen stores, in the entosymbiotes.

Lipid has the advantage over glycogen as a long-term energy reserve in that it allows more calories to be stored per unit weight of tissue or, conversely, less weight need be added per unit energy stored. Energy storage is essential in species likely to experience prolonged periods of hardship, and lipid accumulation

with concomitant increase in calorific value occurs, for example, in birds (Odum, Marshal and Marples, 1965) and termites (Wiegert and Coleman, 1970) prior to migration. It has also been suggested that lipid storage is an adaptation for locomotion, because of the favorable weight/potential energy ratio (Stetten and Stetten, 1956) and this argument could be applied in the case of the free-living flatworms. The principal cause, though, behind the transformation of excess energy into lipids in the free-living species must be that it increases the chances of progeny survival by allowing individuals to survive poor feeding conditions and then subsequently breed. This strategy is obviously advantageous in iteroparous organisms like the triclad Turbellaria, which breed more than once in their life span. Here, survival of adults that might already have bred is equally as important as survival of juveniles. This is in contrast to semelparous organisms, breeding only once in the life span, where juvenile survival may be more important than preservation of adults that might already have bred (Calow, 1973). Some acoel and rhabdocoel turbellarians are semelparous and it would be interesting to compare lipid and glycogen contents and calorific values in these at various stages in the life history. In freshwater molluscs, however, which are similarly semelparous glycogen storage predominates and in fact increases in preparation for over-wintering (Goddard and Martin, 1966). These animals, though, are slow-moving, which permits the storage of less potential energy per unit weight (*vide* Stetten and Stetten, 1956), and they are also herbivorous. This habit, as opposed to the carnivorous one, reduces the probability of either prolonged or intense starvation (Hairston, Smith and Slobodkin, 1960) so that long term energy stores, *i.e.* lipid, are less important.

The triclads utilize lipid during starvation (Jennings, 1957; Boddington and Mettrick, 1971) and, as shown in the present study, this is accompanied by a decrease in calorific value. The importance of this ability, coupled with the triclad's capacity to resorb its tissues and then grow again when conditions permit, has been demonstrated in a classic study by Reynoldson (1966). Reynoldson showed that hatching of the eggs, in European triclad populations, is followed by gradual development of food shortage as the young grow. This slows and eventually stops breeding. The triclads then decline in size, resorbing their tissues, and this is accompanied by some mortality which readjusts population size to food supply. The survivors are then able to feed, grow and reproduce in a further cycle, as conditions permit.

The symbiotic flatworms, and especially the parasitic species, are buffered from such variations in food supply. Ectocommensals are perhaps the least buffered, for their nutritional physiology resembles that of free-living species (Jennings, 1968, 1973). In the species studied here the calorific value is higher than the mean for the ectoparasites (Fig. 1), which have a more stable food supply, but it is still lower than that of the free-living species. In entosymbiotic species, as in the ectoparasites, the food supply is relatively stable. The entocommensals feed on protozoa and other small organisms which are either co-commensals or components of the host's food; in both cases they are abundant and readily available to the entocommensal flatworm (Jennings, 1973). In the entoparasitic species the stability of the food supply is self-evident for tissue-feeders and sanguivores (Monogenea and Digenea), and this is also the case for the

Cestoda which live, almost without exception, in the intestine of vertebrates. Here the host actively maintains a constant level of amino acids, vitamins and other organic substances in the gut lumen, by means of the exocrine-enteric circulation (Read, 1950; Read, Simmons, Campbell and Rothman, 1960; Nasset and Ju, 1961; Nasset, 1965; Read, 1970), and this will buffer the cestode from any temporary changes in the quantity or composition of the host's ingesta.

The adoption of an entosymbiotic life style, therefore, removes the need for long-term storage products because it makes available a stable source of food. The entosymbiote is freed from the need to form lipid reserves to ensure survival until it can breed and we suggest that this is the prime reason for the reduced calorific values of entosymbiotic flatworms. These reduced values may also be related to the fact that entosymbiotic species, once mature, tend to breed more or less continuously throughout their life span and thus will be continually exporting lipid as a component of the eggs. Free-living species, whether semelparous or iteroparous, do not have this prolonged reproductive phase and their relatively high lipid content could be due to a build-up of lipid which is subsequently exported during reproduction. A comparable situation is seen, for example, in freshwater animals which accumulate inorganic salts before breeding for incorporation in the eggs. This hypothesis cannot be tested, as yet, due to lack of appropriate data. We suggest, though, that even if it were proved to be correct it could account for only a proportion of the discrepancy between the calorific values of symbiotic and non-symbiotic flatworms, and that reliability of the food supply is the major factor.

The food supply of entoparasites would seem to be even more reliable than that of entocommensals, and so the evolution of entoparasitism is seen as a logical conclusion to the tendency to form symbiotic associations which is a dominant feature of the biology of the Platyhelminthes.

The entosymbiotic life style, though, places a very considerable premium on production of offspring, because of the problems of dispersal between hosts. This can be met by using resources that in free-living flatworms would have to be diverted into lipid reserves. Such increased production of progeny presumably involves considerable expenditure of energy and since long-term storage is not involved glycogen rather than lipid is the most suitable substrate. It is readily metabolized and its high molecular weight and low intrinsic viscosity permit accumulation in tissues without much effect on osmotic pressure (Stetten and Stetten, 1956). Thus, although there may be fairly rapid turn-over of glycogen in entosymbiotes that are continually producing eggs, its properties are such that the tissues can always contain relatively large amounts.

The occurrence of large quantities of glycogen in entosymbiotes appears, therefore, to be basically an adaptation for high fecundity, necessitated by the mode of life, and is not primarily an adaptation related to environmental oxygen tension, as has been previously suggested. Nevertheless, as pointed out by Jennings (1973), the presence of glycogen in entosymbiotes does constitute a pre-adaptation for life under conditions of low or variable oxygen tension, in that a suitable substrate is already available for partially or totally anaerobic respiration. A number of entosymbiotic flatworms, notably the Cestoda, have exploited this potential and colonized habitats such as the vertebrate intestine where the oxygen concentration may be much reduced. In such species there is, without doubt, a direct

relationship between their high glycogen content, the low environmental oxygen tension, and their modified respiratory physiology, but on the above argument this relationship is seen to be proximate rather than ultimate in nature.

An interesting consequence of our interpretation of the relationship between the nature of the food reserve, mode of life and level of fecundity, is that parasitism, and especially entoparasitism can be regarded simply as adaptive devices which favor high fecundity. This view, of course, is the reverse of the classical view, already cited, that high fecundity is a basic and essential adaptation for the parasitic habit.

In explaining the distribution of calorific values within the Platyhelminthes we have emphasized the importance of reproductive strategy and food availability. This is because groups with different life styles, ranging from completely parasitic to completely free-living, fit exactly into the distribution spectrum from low to high caloric values and we believe that the only parameters which show the same distribution are fecundity and food availability. We dismiss the direct involvement of oxygen tension for reasons already stated but accept that mobility might be of some importance. For example, free-living forms may need to be more mobile than parasites and thus might require to store more energy per unit weight. This could account for their higher calorific values. However, such an argument presupposes that food stores are necessary anyway, and in this sense is less basic than our explanation in terms of fecundity and food supply. Furthermore, the two possibilities are not mutually exclusive.

There may, of course, be more subtle explanations. For example, there could be some biochemical disadvantages (other than those stemming from reduced oxygen tension) associated with lipid storage, and hence high calorific values, in the enclosed entosymbiotic environment. It is difficult, though, to envisage what these could be and so we present our argument as the most plausible within the limits of currently available information.

Summary

1. A comparison has been made of the calorific values (kcal/g ash-free dry weight) of 21 species of flatworms which exhibit, between them, the various life styles found in the phylum Platyhelminthes.

2. The grand mean calorific value for whole animals of all 21 species was 5.841 ± 0.230 kcal/g ash-free dry weight, which is close to the mean of 5.821 kcal/g ash-free dry weight reported for whole animals from a wide range of other phyla.

3. There is a direct relationship between mode of life and calorific value. Free-living flatworms have a mean value higher than the mean for whole animals in general, while entocommensal and entoparasitic species other than cestodes have

lower values. The ectocommensal, ectoparasites and cestodes have values close to the mean.

4. In the cestode *H. diminuta* the values for immature and mature proglottids (regions comparable to whole flatworms from other classes) are less than the mean for whole animals from other phyla and approach those for the entocommensal and entoparasitic flatworms. Gravid proglottids have a higher mean.

5. The entosymbiotic flatworms, with high fecundity relative to free-living species, thus conform to the hypothesis that fecundity is linked with low potential energy per unit weight.

6. The dichotomy in food reserves in the Platyhelminthes, with storage of lipid in free-living species and of carbohydrate in the symbiotic forms is considered, therefore, to be basically an adaptation to different reproductive patterns necessitated by different life styles.

7. It is suggested that the emphasis on carbohydrate as an energy source, rather than lipid, pre-adapted entosymbiotes for partial or total anaerobic respiration. The relationship between high glycogen content, low environmental oxygen tension and modified respiratory physiology occurring in some entoparasites is thus proximate rather than ultimate in nature.

8. The evolution of entoparasitism is seen as a logical conclusion to the trend toward the formation of symbiotic relationships, which is a characteristic feature of the Platyhelminthes, in that it removes the need for long-term reserves and thereby allows total emphasis on progeny production. It follows that the parasitic habit, and especially entoparasitism, provides conditions necessary for high fecundity so that the latter can be regarded as a direct and automatic consequence of the parasitic mode of life, rather than as a specific adaptation to it.

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